VARIATION IN THE TEETH OF NEREIS.

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THE purpose of this quantitative study in variation is to determine the modal condition of a character in a species of Nereis commonly found on the west coast of the Atlantic. The material was very generously placed at my disposal by Professor Charles B. Davenport, who collected it during the summer of 1899 at Cold Spring Harbor, Long Island. The animals were found in the sand of the beach and were taken at random, excepting that small ones were rejected.

These annelids went by the familiar name of *Nereis virens*, but upon comparing them with Ehlers's ('68, p. 559) descriptions and drawings of that species, I found that although they agreed in most characters, an important difference occurred in the length of the first or postoccipital segment; that of *N. virens* being twice as long as the second segment, while that of the Cold Spring Harbor form is about equal to or even slightly less than the second in length. In this character, as also in that of certain parapodal bristles, the "Sichelanhänge," which are rather short and broad instead of slender and long as in *N. virens*, the Cold Spring Harbor species agreed well with Ehlers's description of *N. limbata*, the distribution of which also includes the west Atlantic coast. From these two points, and from the fact that Cold Spring Harbor is slightly south of the southern limit described for *N. virens*, and within the range of *N. limbata*, it seems probable that we are here dealing with the latter of Ehlers's two species. It may be possible that the two species overlap in this region at the southern limit of *N. virens*, and that my collection contained both. However, nothing in the numerical results of my investigation seemed to suggest two distinct or even transitional forms.

1. *Method.*

The specific character selected for investigation was the number of teeth on the jaw. This number is commonly stated by authors in descriptions of species.

The jaws are two in number, from 1 to 3 mm. in length, brown, horny, curved, and serrated along the inner or falcate margin. They are at the extremity of a large exsertile proboscis which is usually retracted in alcoholic specimens, so that in order to free the jaws it is necessary to cut down the median line of the head, ventrally, through to the inside of the muscular proboscis. By turning the head backwards the jaws can be made to extrude, and the teeth counted by means of a hand lens. In the specimens killed later in the season by a slowly killing fluid, the jaws remained extruded.

In counting, some difficulty was experienced in fixing a limit in either direction, at the curved, distal end in those cases in which very fine teeth ran to the tip, and particularly at the proximal extremity where the outlines of the teeth were indefinite. In order to count these it was necessary to pull out the jaws gently with a forceps, and to free the bases from connective tissue, carefully, without entirely separating the jaws from the head. Since the line of division between the free, prominent teeth and the undeveloped ones, buried in a chitinous band, was always distinct, the method was adopted of counting them separately, and of including in each set all that showed well-formed outlines when held up against a strong light and viewed through a lens from the dorsal side. Those connected by the chitinous band were called indefinite teeth, the rest the definite teeth. Totals were found by adding.

2. *Results.*

I. TABLE OF DISTRIBUTION OF FREQUENCIES.

Classes	1	2	3	4	5	6	7	8	9	10	11	12	13	14
L. Def. . .		5	30	88	128	102	41	6						
L. Indef. .		12	30	93	146	93	21	4	1					
L. Total .						3	12	28	95	116	100	39	7	
R. Def. . .	1	4	37	94	126	86	41	11						
R. Indef. .	2	7	30	80	149	97	28	7						
R. Total .					1	2	8	27	102	114	89	46	10	1

From the table of frequencies it will be seen that the number of definite teeth varies from 1 to 8, the indefinite from 1 to 9, the total numbers from 5 to 14.

The following constants were obtained.

II. TABLE OF CONSTANTS.

	LEFT DEF.	LEFT INDEF.	LEFT TOTAL.	RIGHT DEF.	RIGHT INDEF.	RIGHT TOTAL.
n	400	400	400	400	400	400
M	5	5	10	5	5	10
A	5.098 ± 0.040	4.905 ± 0.039	10.00 ± 0.044	5.043 ± 0.043	5.013 ± 0.040	10.055 ± 0.045
σ	1.193 ± 0.028	1.179 ± 0.0279	1.306 ± 0.031	1.267 ± 0.030	1.191 ± 0.028	1.339 ± 0.032
F	+ 0.7025	− 0.66148	+ 0.0599	+ 0.4339	− 0.8617	− 0.5314
Type	I	IV	I	I	IV	IV
Skewness	− 0.0369	− 0.0439	− 0.1341	+ 0.0153	− 0.0868	− 0.0509

Comparison of these numerical results suggests the following conclusions:

The mode, 5, is the same for the definite and indefinite on both sides, and for the total on each side it is 10. The averages also show little difference between the right and left jaws. From the variability, however, as indicated by the standard deviation, it appears that the number of teeth of the right jaw is slightly more variable than that of the left, σ being 0.074 greater on the right side for the definite teeth, 0.011 (which is less than the probable error) for the indefinite teeth, and 0.033 greater for the right total. The highest degree of variation is shown by the total number of teeth on the right side, and the least variation is shown by the number of indefinite teeth.

The form of the distribution curve of definite teeth on both jaws falls under Pearson's Type I, with the peculiar result of a slight negative skewness for the left side, and a positive skewness, although a very slight one, +0.0153, for the right. This indicates a tendency to the production of fewer definite teeth than normal on the left side, and a faint tendency towards a greater number on the right side. The distribution curve of indefinite teeth on both sides is of Type IV, with a negative skewness, −0.043, on the left side, and twice this, −0.086, on the right; *i.e.*, there is on the right side a greater

tendency than on the left towards the production of few indefinite teeth. On the right side, then, it is clear that the probability of a large number of definite teeth is associated with that of a small number of indefinite teeth. The same thing is shown for the left side, for although definite and indefinite teeth both show negative skewness, the negativeness is much greater in the indefinite than in the definite teeth. Therefore, relatively, the skewness of the indefinite and the definite teeth may be said to be, here also, of opposite sense. This agrees with results shown in the correlation table, to be noted later.

A peculiar result is obtained in regard to the distribution curve of the total number of teeth. The left total falls into a curve of Type I, while the right total is of Type IV. The negative skewness of the latter is -0.050, while that of the former is about two and one-half times as much. The table of frequencies shows that the right total includes two classes more, one at each end of the series, than the left total. There is one individual in each of these two classes. It seemed probable, by inspection of the calculation, that the critical function, F, which was negative 0.5314, might be made positive by dropping these two extreme individuals, thus giving a curve of Type I. I found this to be the case, and obtained for F the value $+0.210$; but I found further that Type I might be obtained by dropping only the individual of Class 5, making F $+0.0389$. The skewness in this case was very slight, only -0.00706.

In order to determine which was the closer fit of the observed curve to the theoretical curve in the two types, I calculated the theoretical curves from the observed data with the following result.

TYPE IV.[1]

$n = 400$	$d = 0.06822$	$M = 10.055$
$s = 25.66$	$m = 13.830$	$y_0 = 96.34$
$a = 6.5798$	$\sigma = 1.3386$	zero ordinate = 9.1114 (M-md)
$v = 3.6796$	$\phi = 8° 9' 7''$	$\tan \theta = x/a$

$$y = y_0 (\cos. \theta)^{2m} e^{-v\theta}$$

[1] For the methods of calculating the results given in the following tables, see Davenport, '**99**, pp. 20, 23, 24.

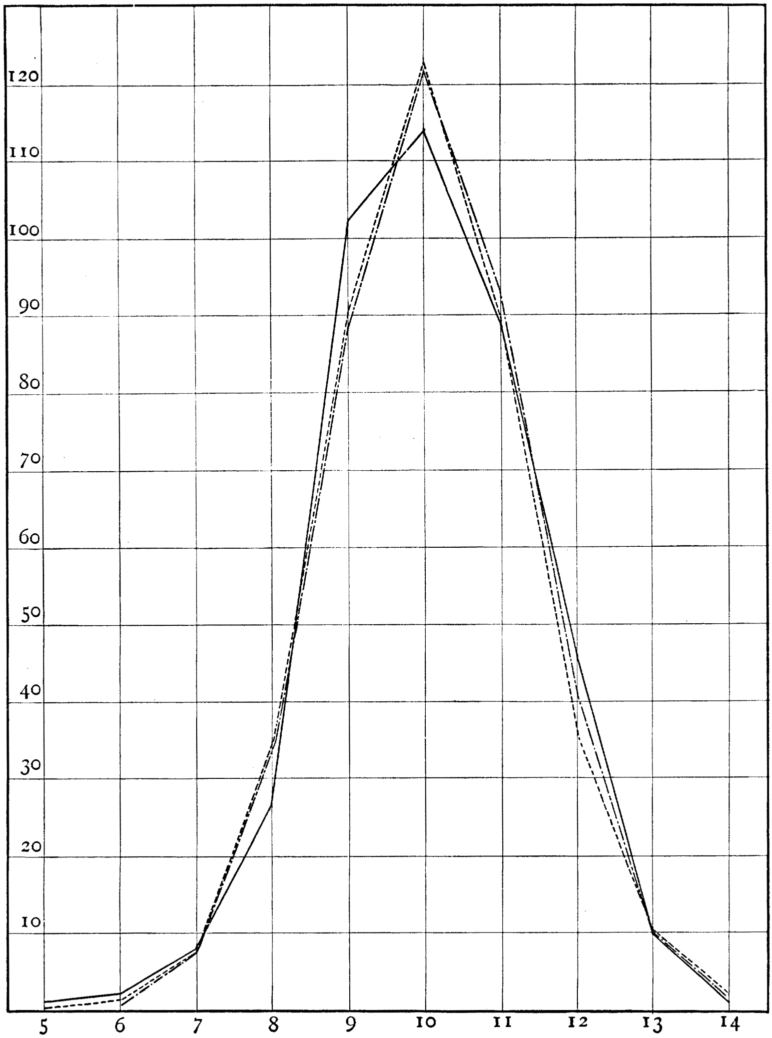


PLATE I.

——— Polygon of observed frequency.
······· Polygon of theoretical frequency, Type IV.
—·—· Polygon of theoretical frequency, Type I.

Δ, Calculated by Duncker's method, = 3.68%.

V–M	*f*	*y*	δ_1	δ_2
− 4.1114	1	0.1	+ 0.87	
− 3.1114	2	1.2	+ 0.8	
− 2.1114	8	7.9	+ 0.1	
− 1.1114	27	35.3	− 8.3	− 0.09
− 0.1114	102	90.5	+ 1.5	− 4.82
+ 0.8886	114	122.9	− 8.9	− 5.01
+ 1.8886	89	89.9	− 0.98	
+ 2.8886	46	35.5	+ 7.43	− 0.85
+ 3.8886	10	10.8	− 0.89	− 0.79
+ 4.8886	1	2.3	− 1.36	
	400	399.7	41.05	11.56

TYPE I.

$n = 399$ $\quad s = 305.56$ $\quad b = 46.165$

$a_1 = 21.663$ $\quad m_1 = 142.426$ $\quad \sigma = 1.316$

$a_2 = 24.502$ $\quad m_2 = 161.134$ $\quad d = 0.00929$

$y_0 = 120.68$ (calculated from approximate formula). $\quad M - d = 10.066$

$$y = y_0 \left(1 + \frac{x}{a_1}\right)^{m_1} \left(1 - \frac{x}{a_2}\right)^{m_2}$$

Δ, Calculated by Duncker's method, = 3.58%.

V–M	*f*	*y*	δ_1	δ_2
− 4.066	2	0.9	+ 1.07	
− 3.066	8	7.8	+ 0.2	
− 2.066	27	35.2	− 8.24	− 0.19
− 1.066	102	87.2	+ 14.84	− 5.29
− 0.066	114	121.5	− 7.46	− 4.96
+ 0.934	89	93.1	− 4.08	
+ 1.934	46	41.1	+ 5.06	− 2.25
+ 2.934	10	10.3	− 0.3	− 0.29
+ 3.934	1	1.4	− 0.42	
	399	398.5	41.60	12.98

Since it is considered a sufficient agreement between observation and calculation when $\Delta < \frac{100}{\sqrt{n}}$ %, which in this case is 5 %, it is evident that these values show a moderate degree of closeness of fit of the two curves. The difference between the two values of Δ, 0.10, is so small that we may conclude that it is practically immaterial under which type this curve should fall.

The fact that by dropping one individual from a series a curve may be thrown from Type IV to Type I and may be made to fit equally well in either case, raises a serious question as to the biological importance of the distinction between Pearson's Type I and Type IV. Pearson ('95) himself says: "It seems very possible that discreteness rather than continuity is characteristic of the ultimate elements of variation; in other words, if we replaced the curve by a discrete series of points, we should find a limited range. It is the analytical transition from this series to a closely fitting curve which replaces the limited by an unlimited range. Exactly the same transition occurs when we pass from symmetrical point binomial to normal curve. Thus while Type I marks an absolutely limited range, Type IV does not necessarily mean that the range is actually unlimited."

It appears from the results obtained in the two calculations given above that even less value can be placed upon any distinction between Type I and Type IV than is suggested by Pearson. The difference of one individual actually causes, here, the transition from one type to the other, the individual being at the extreme of the series.

3. *Correlation.*

In the table on the following page every possible combination of teeth for the two sides is given, together with the actual number of specimens for each combination of definite, indefinite, and total teeth.

From this series of combinations the following results were obtained for the coefficient of correlation. The calculations were made by Pearson's method and checked by the briefer method of Duncker.

Correlation between Right and Left Definite Teeth,	$r = +0.688 \pm 0.0136$
" " " " " Indefinite "	$r = +0.725 \pm 0.0121$
" " " " " Total "	$r = +0.820 \pm 0.0081$
" " Right Definite and Left Indefinite,	$r = -0.424 \pm 0.0231$

Bearing in mind that an index of 1 signifies a perfect correlation, and that 0 indicates an entire lack of it, we see that the

III. CORRELATION TABLE.

Teeth.		Specimens with definite teeth.	Specimens with indefinite teeth.	Teeth.		Specimens with definite teeth.	Specimens with indefinite teeth.	Teeth.		Specimens with total teeth.	Teeth.		Specimens with total teeth.
R.	L.			R.	L.			R.	L.		R.	L.	
1	2		2	5	5	67	79	5	6	1	11	9	1
1	4	1		5	6	26	20	6	6	2	11	10	20
2	2	2	5	5	7	6	2	7	7	7	11	11	60
2	3	1	2	5	8		1	7	8	1	11	12	7
2	4	1		6	3	2		8	7	4	11	13	1
3	2	2	4	6	4	8	5	8	8	13	12	9	2
3	3	14	12	6	5	17	32	8	9	8	12	10	5
3	4	14	11	6	6	49	54	8	10	2	12	11	14
3	5	6	2	6	7	9	7	9	8	11	12	12	23
3	6		1	7	4	1		9	9	61	12	13	2
3	7	1		7	5	4	5	9	10	25	13	12	6
4	2	1	1	7	6	13	15	9	11	5	13	13	4
4	3	7	9	7	7	21	8	10	7	1	14	12	1
4	4	41	39	7	8	2		10	8	3			
4	5	36	27	7	9		1	10	9	23			
4	6	9	4	8	6	3		10	10	64			
5	3	6	8	8	7	5	3	10	11	21			
5	4	22	38	8	8	3	3	10	12	2			
						400	400						400

degree of correlation between the right and left sides is, on the whole, rather high. It seemed at first a somewhat unexpected result that the correlation in the variability of what I have called the indefinite teeth should be higher than in that of the definite teeth. If the correlation had been perfect it would have meant that those causes which produced a deviation from the mean in the left sets acted in the same degree on the right sets also. Is it possible then that different causes may have acted or that the same cause may have been effective in different degrees in producing the variability in the definite and the indefinite teeth ?

This question drew my attention more closely to a fact noticed only incidentally in counting the teeth, *i.e.*, in case of animals having dark, heavy jaws, evidently older animals, the definite teeth were fewer in number than in case of small, young individuals. In the older jaws the teeth began farther from the tip, leaving a smooth point, while the younger, more

delicate jaws were often finely denticulated to the extremity. The serratures of the older jaws appeared to be worn off by use. In order to determine whether or no the correlation actually existed between the size or age of an animal and the number of definite teeth, I made the comparison for one hundred individuals, taking as an indication of size, and hence roughly of age, the head length in millimeters. This was measured from the anterior edge of the first ring to the extremities of the two apical feelers. The result was a negative correlation, although a rather small one, -0.128. It is probable, then, that age does come in as a factor in the production of a small number of teeth, and that this decrease is due to wear. It is possible also that the wear may be heavier upon one jaw than upon the other, thus accounting for the comparatively slightly lower degree of correlation between the definite teeth than between the indefinite teeth. For wearing does not act at all directly on the indefinite teeth, since they do not emerge from the chitinous covering, and are often sunk in the tissue of the proboscis. It would be interesting to know in what manner the jaws are carried and work upon each other during the life of the animal, for a certain habit of crossing them might also account for the peculiar differences in skewness of the curves of the right and left teeth noted in the discussion of constants. The smallness of the negative index of correlation between the age of an animal and the number of definite teeth shows that age does not play a very important part in causing variation.

An attempt to correlate the number of definite and the number of indefinite teeth on the right jaw resulted in a negative index of correlation, -0.424. This fact indicates an inverse relation between the definite and indefinite teeth on the same jaw; that is, a jaw with a small number of definite teeth will probably have a comparatively large number of indefinite teeth, and inversely. It may be that indefinite teeth continue to be laid down at the base of the jaw during the life of the animal, in which case the number would tend to be greater with age, while, as we have seen, the number of definite teeth is smaller.

4. *Relation of Individual and Specific Variation.*

Out of fifty different species of Nereis which I found described by various authors, the number of teeth was stated for forty-seven. The numbers ranged from 0 in two cases, in which the edentalous condition of the jaws was an important specific character, to 20, given by Audouin and Milne-Edwards ('29) for *N. fucata*. The number of teeth of *N. fucata* is given by Ehlers ('68), however, as 7, by Johnston ('65) as 5 to 10, and in the Challenger ('85) reports as 14 to 16. It would be difficult here, as in the case of a few others, to decide which observer came nearest to the modal condition of the species. It is also impossible to tell whether they counted the total number of teeth including those covered by a chitinous band, or whether they referred only to the prominent definite teeth. Ehlers makes the distinction only in *N. virens*, where he gives the definite teeth as 5 to 6, total as 10. St. Joseph ('88, '98) notes in description of *N. diversicolor* that of 8 teeth 2 are indefinite, and in *N. floridana* that of 9 teeth the lower 4 are buried in a clear translucent covering. For these two species, respectively, Ehlers has given 8 and 9 teeth, evidently counting both definite and indefinite.

After attempting various methods of striking averages of the statements made by different authors I finally decided to use Ehlers's numbers alone as most reliable, adding a few of those given by St. Joseph in which there was less doubt that the total number of teeth had been counted. Seriation of twenty-two species gave the following results, total teeth.

Classes . . .	5	6	7	8	9	10	11	12
Frequencies	1	1	5	2	6	3	2	2

CONSTANTS.

A = 8.727	F = + 1.354
σ = 1.838	curve = Type I
β_1 = 0.000090	s = 5.862
β_2 = 2.323	skewness = + 0.00966

Any conclusions which can be drawn from these results are necessarily of doubtful value. It will be seen that the mean

for the number of teeth in twenty-two species is lower than the mean of total teeth in the one species which I have described. The skewness of the curve instead of being negative is positive, although it is exceeding small. Had it been negative, as I had thought it might be, it would have indicated that in the species of the genus, as well as in the individuals of the species, there had been a movement in the direction of a smaller number of teeth, either from an excessive production of individuals and species having few teeth, or from selective annihilation of those having many teeth. The opposed positive skewness is so small that it may mean little in regard to the species, and particularly since the numbers are small and the method of counting so doubtful no stress can be laid upon it.

5. *Abnormalities.*

Differences between the two jaws of the same animal in the definite, indefinite, or total number of teeth were of common occurrence. The accompanying drawings are intended to show some irregularities of this kind. In Fig. 1 the right jaw has four large definite teeth and five below which do not emerge from the surrounding chitinous layer; the left jaw has only slight crenulations corresponding to five definite teeth, although it has the same number of indefinite teeth as the right side. Fig. 2 shows on the right jaw three definite teeth, the edge above and distal to them having three very slight elevations; the opposite jaw ends in a long point with a perfectly smooth edge and has only two large definite teeth below. There is the same number of indefinite teeth on both sides. Figs. 3 and 4 show variations of the same kind, the numbers of both definite and indefinite teeth being different for the two jaws.

So far the drawings have been made from old animals in which the jaws are hard, strong, and very dark in color. It is probable from the appearance of the jaws that the difference in the number of definite teeth is due largely to the wearing, on one side or the other, of the distal teeth. Fig. 5 shows a common irregularity of equal totals with slight differences in

the combinations of definite and indefinite teeth, the left jaw having 8 to 4, the right 6 to 6. Figs. 5 and 6 are from small, young animals, and the jaws are seen to be more slender with numerous fine teeth, 13 on the right and 12 on the left jaw.

The specimen drawn in Fig. 7 was interesting in regard to the indefinite teeth. The left jaw presented the usual appear-

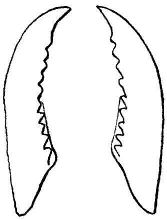


FIG. 1.

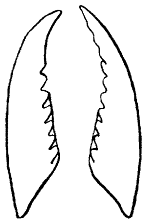


FIG. 2.

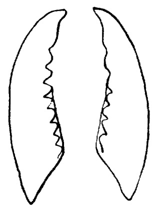
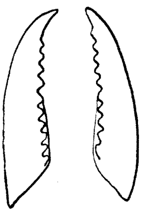


FIG. 3.



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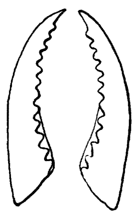

FIG. 5.

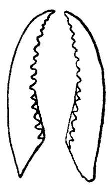

FIG. 6.

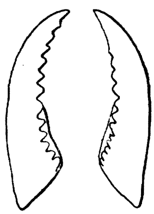

FIG. 7.

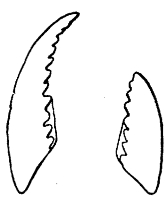

FIG. 8.

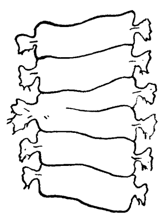

FIG. 9.

PLATE II.

FIGS. 1–8. — Variation and abnormalities in teeth on opposite jaws.
FIG. 9. — Abnormal segment.

ance of six indefinite teeth placed fairly regularly and six definite teeth. On the right jaw the point was worn smooth, leaving only four definite teeth, while below three normal indefinite teeth was a series of five small ones placed very close together instead of three as on the opposite jaw. This may indicate a tendency towards regulation by the production

of an excess of teeth at the base of a jaw on which some of the extreme teeth had been lost, but I found no other indication of such regulation. Another individual presented a partial right jaw, Fig. 8, which was a stump of about half the length of the left jaw. The normal jaw was dark brown, almost black, while the stump was light straw color characteristic of a young jaw or of the very base or imbedded part of an old one. The color indicated new growth or regeneration, in which case one would expect to find a production of small indefinite teeth crowded at the base, as in the specimen of Fig. 7, if that could be interpreted as a regenerative process. On the contrary, the stump had exactly the same number of teeth similarly disposed as the part of the opposite jaw which corresponded to it. It may have been, then, only the rounded stump of a broken jaw, although this explanation does not account for the peculiar color.

Abnormalities in other parts of the animals were looked for only incidentally. I found no cases of double pairs of caudal cirri, but all of the worms were not examined for this not unusual abnormality, since the posterior parts of many of them were not preserved.

Fig. 9 shows a case of an abnormal segment. The fifteenth segment extended only a little more than halfway across towards the left side of the body, leaving one broad segment on the left side in place of two, and a partially double parapod. The axis of the body was bent at that point, compensation being made gradually by the greater width on the left side of the segments immediately preceding and following.

6. *Summary.*

The results of this study may now be summed up as follows:

(1) The typical condition for the total number of teeth of *N. limbata* of Cold Spring Harbor, 1899, is a curve of either Type I or Type IV, with a slight skewness in a negative direction from the mode, 10.

(2) In case of the calculation of the right total teeth, a transition from a curve of Type IV to an equally serviceable

one of Type I could be made by discarding one extreme individual out of four hundred.

(3) The number of teeth on the right jaw appears to be slightly more variable than that on the left.

(4) The degree of correlation between the two jaws is, on the whole, rather high, 0.820. Correlation is closer between the indefinite than between the definite teeth. An inverse relation exists between the number of definite and the number of indefinite teeth on the same jaw, and also one between the number of definite teeth and the age of an animal.

(5) The class range of teeth as given by the different species of the genus Nereis has a close agreement with the class range of *N. limbata.* Hence this one species offers the material for the modal condition of all species of the genus.

(6) The results of observations of many specimens showing irregularities in teeth point to the conclusion that a process of wearing away of the definite teeth takes place in mature animals, and therefore that age comes in to help produce small number of teeth, but is not a large factor in causing variation.

Only one author, St. Joseph, makes note of a difference between young and old specimens, the young having the greater number of teeth. Thus the statements made in regard to the number in many species in which only one animal or at most very few specimens were seen and described by their discoverers, are of little value as criterions of the specific condition.

In conclusion, I wish to express my thanks to Professor Charles B. Davenport, who not only generously furnished the material for this investigation, but by his oversight and advice greatly facilitated the progress of the work.

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